

THE PODOSTEMACEAE IN THE SOUTHEASTERN
UNITED STATES¹

S. A. GRAHAM AND C. E. WOOD, JR.

PODOSTEMACEAE L. C. Richard ex C. A. Agardh, Aphor. Bot. 125. 1822,
"Podostemeae," nom. cons.

(RIVERWEED FAMILY)

Moss- or alga-like, submerged aquatics, generally restricted to sunny, clear, swiftly flowing streams and waterfalls of the tropics and subtropics. Plant body often reduced to a "thallus" and anchored to the rock substrate by cement-secreting root hairs and haptera (specialized rootlike organs that act as holdfasts). Stems present [or lacking]. Leaves alternate, simple to much divided. Inflorescences diverse, the flowers solitary [or fasciculate or in a 2-sided spiciform monochasium], [enveloped by a few leaves or] entirely inclosed within a membranaceous spathella (or "spathe") that ruptures irregularly as the pedicel elongates before anthesis. Flowers [actinomorphic to] zygomorphic, perfect. Perianth of 2 or 3 [or 5 to many] tepals (staminodes?), [petaloid to] reduced and scalelike. Stamens [1 or] 2 [to many]; anthers 4-loculate; pollen commonly in dyads [monads or polyads]. Gynoecium [1-], 2- [or 3-] carpellate, syncarpous; ovary superior, [1-], 2- [or 3-] loculate; ovules [2 to] many, on an axile placenta. Fruit a septifragal [or septicidal] capsule; seeds many, without endosperm; embryo straight. TYPE GENUS: *Podostemum* Michx.

¹Prepared for the Generic Flora of the Southeastern United States, a joint endeavor of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation. This treatment, the seventy-seventh to be published, follows the format established in the first paper in the series (Jour. Arnold Arb. 39: 296-346. 1958). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with additional material in brackets []. References that we have not seen are marked by an asterisk.

The manuscript for this account was originally prepared when the first author was a member of the Generic Flora project in Cambridge in 1963-64 (NSF Grant GB-171, C. E. Wood, Jr., principal investigator). Since only a single species was involved, and the New World members of the family had been recently revised, publication was delayed pending the addition of other material and the preparation of a suitable illustration. The manuscript has been revised and updated by the second author (under NSF Grant BMS 74-21469). Since the family is one of great biological interest and since the numerous references are rather widely scattered, an unusually large number of references (out of all proportion to the representation of the family in our flora) are presented here. The illustration was drawn in April, 1975, by Karen S. Velmure under the supervision of Kenneth R. Robertson, who also prepared the dissections. The liquid-preserved material from which figures *a* to *h* were drawn was collected in North Carolina by S. W. Leonard and William Waterfield and came to us through the kindness of S. A. Spongberg and R. E. Weaver, respectively.

A remarkable pantropical family of highly modified submerged aquatics, including about 45 genera and 200 species, many of these narrow endemics, a few widely distributed. Almost all are restricted to rocky substrates in clear, sunlit, swift-running streams and rivers, where they occur especially in waterfalls and rapids. About 140 species are known from the Americas, 40 from Africa, and 20 from Asia (northward to southern Kyushu, Japan) and Australia (Queensland). *Podostemum ceratophyllum* Michx., one of the few representatives of the family in temperate regions, occurs in the southeastern United States.

The unique habitat of these plants is shared by hardly any others, except Hydrostachyaceae. The family is notable for a high degree of speciation and endemism, with several species and some genera known only from a single rapids or cataract, and with some closely related species occupying adjacent tributaries of the same river or nearby rivers (Van Royen, 1951, p. 13). A few exceptional species, including *Podostemum ceratophyllum*, are widely distributed. *Tristicha trifaria* (Bory ex Willd.) Sprengel is noteworthy, extending as it does from Cuba to Mexico, southward to Uruguay and Argentina, and over a large part of Africa to Madagascar.

The plants flower as the water level recedes (usually with the onset of a dry season) and as they become exposed to the air. Pollination is usually by insects or wind and is followed by very rapid fruit development, in some cases the fruit maturing in as little as 24 hours (e.g., in *Apinagia*; see Went, 1926, 1929). The seed coat is mucilaginous when moistened and adheres to the substrate, where the seed germinates if it is not washed away as the water level rises (cf. *Podostemum*). *Polypleurum submersum* J. B. Hall is a rare exception in the family in that it grows in still rock pools in the River Asuboni, Ghana, prospering "even in pools that are stagnant and separated from the flowing water. Spathellae open under the surface and flowers are pollinated by the current." The fruits dry and dehisce, however, only when exposed to the air.

Podostemaceae are so variable morphologically that it has proved difficult to devise a satisfactory subfamilial classification, although several have been proposed. Most recently, Van Royen (1951) has recognized two subfamilies: Tristichoideae Engler emend. Royen, with flowers enveloped by a few leaves and with a 3- or 5-lobed perianth, and Podostemoideae, with flowers inclosed in a "spathella" and with the tepals reduced to scales. The four tribes (Tristicheae, Weddelineae; Mourereae, Podostemeae), two in each subfamily, are based mainly on characters of the inflorescence, perianth, and stamens.

The relationships of the family Podostemaceae to other families have been the subject of much discussion, leading to its placement near such diverse families as the Piperaceae, Polygonaceae, Caryophyllaceae, Crassulaceae, Nepenthaceae, and Scrophulariaceae. Embryogeny provides strong evidence of its relationships to Crassulaceae and to Hydrostachyaceae, a small family once united with the Podostemaceae. Among the characteristic features of the embryology of the Podostemaceae are the

tetranucleate megagametophyte (embryo sac) that lacks antipodal cells or has only a single one; the absence of endosperm; the growth of the top of the megasporangium (nucellus) beyond the inner integument into the endostomium; the restriction of the megagametophyte (embryo sac) to the upper part of the megasporangium (nucellus), while the lower part elongates to form a pseudo-embryo sac; and the appearance of the outer integument to form the micropyle before development of the inner integument. Maheshwari, drawing support from the earlier embryological studies and conclusions of Mauritzon, has suggested that the Podostemaceae (and Hydrostachyaceae) are derived by reduction from the Crassulaceae, a theory based mainly on the highly developed suspensor haustoria found in both families and the similarities in embryogeny between some aquatic Crassulaceae (e.g., *Tillaea aquatica*) and the Podostemaceae.

In floral morphology the evolutionary trend appears to have been from actinomorphic to zygomorphic flowers, accompanied by a change from entomophily to anemophily or autogamy. A high degree of ovule abortion, of unknown cause, has been reported.

The only chromosome numbers reported are those of *Terniola ceylanica* (Gardner) Tulasne (as *Lawia zeylanica*), $2n = 20$; *Podostemum subulatum* Gardner, $2n = 40?$; and *Weddelina squamulosa* Tulasne, $2n = 40$.

Van Royen notes that plants of this family throw off part of the outer tissues after the water level subsides, producing great changes in appearance and making it difficult to judge herbarium material, in which these same changes can occur during the process of pressing and drying. The best way of preserving specimens is in 60–70 per cent alcohol, in 4 per cent formalin, or in a mixture of the two.

The Podostemaceae are of great biological interest but of no economic importance.

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Subfam. PODOSTEMOIDEAE

Tribe PODOSTEMEAE

1. *Podostemum* Michaux, Fl. Bor. Am. 2: 164. pl. 44. 1803.

Gregarious, dark green to reddish herbaceous perennials of shallow, rushing streams or rapids, firmly attached to rocks or gravel by means of cement-secreting root hairs and fleshy disclike haptera arising from the lower surface of \pm dorsiventral, photosynthetic, horizontal (plagiotropic), creeping, branched roots. Stems present [or lacking], originating in pairs along the sides of the roots, without a growing point, the leaves alternating in two ranks, each leaf arising from the base of the next older leaf in its rank; lateral shoots arising at the base of the leaf on its outer (abaxial) side, not in the axil of the leaf. Leaves distichous, repeatedly forked [or entire], spatulate to mainly filiform, with the exception of the lower leaves with an intrapetiolar stipule. Flowers axillary, solitary on short pedicels, the spathella rupturing at the distal end, the tepals and stamens restricted to the adaxial side of the flower. Tepals (the "staminodes" of some authors) 2 or 3, filiform, acute, one on each side

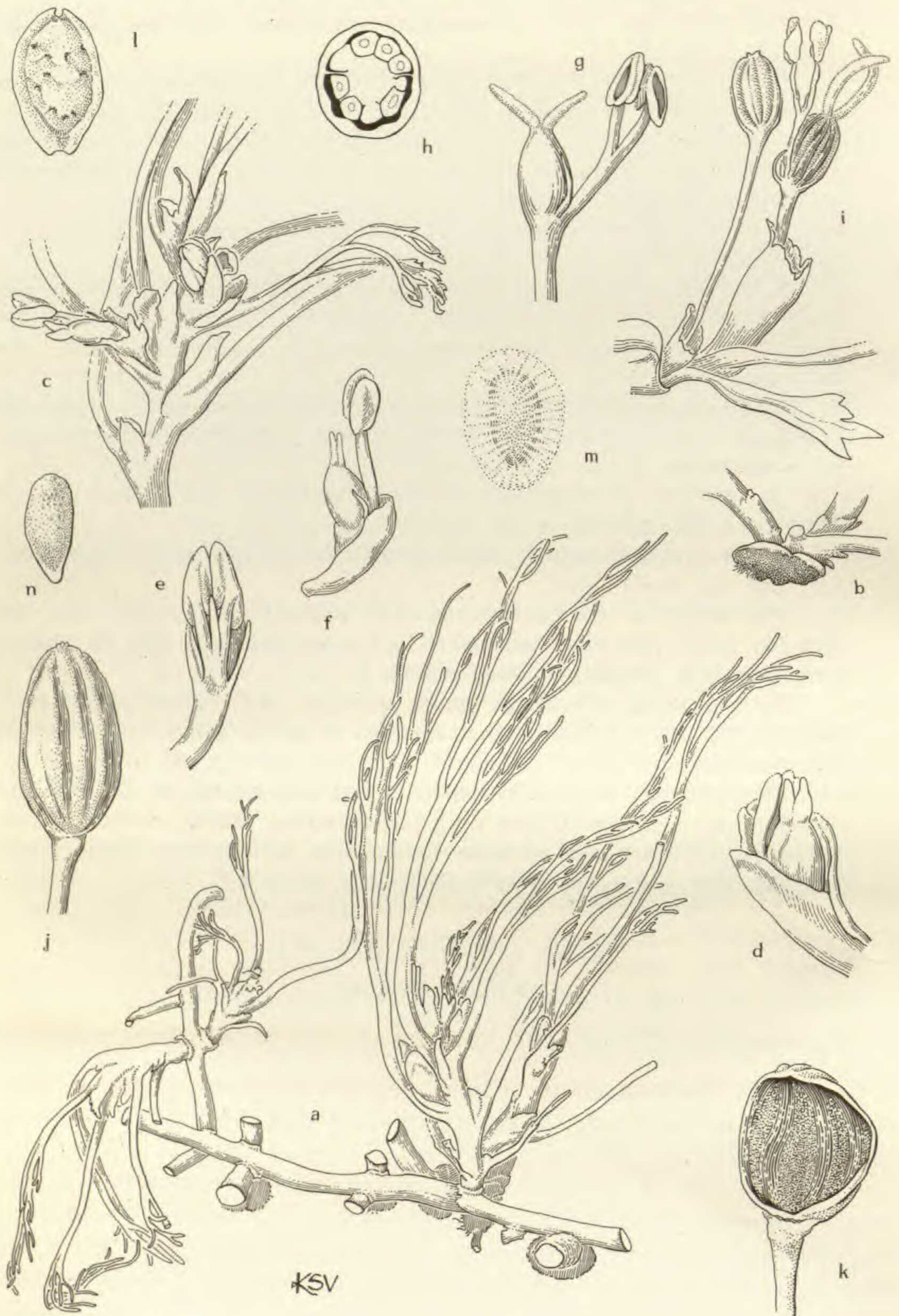


FIGURE 1. *Podostemum*. a-n, *P. ceratophyllum*. a, part of horizontal root with several opposite branches (some removed for clarity), anchoring haptera produced on root below branches, the leaves repeatedly forked, $\times 2$; b, detail of hapteron, $\times 3$; c, detail of branch, showing bases of leaves with intrapetiolar stipules, each flower solitary in a spathella in axil of leaf, $\times 3$; d, young flower emerging from spathella, $\times 6$; e, same flower from behind (removed from spathella), a tepal to each side of androphore and a third inserted on androphore

of the androecium (partially fused filaments, androphore, andropodium), the third (the "scale" of some authors), when present, in the fork between the filaments of the two stamens. Androecium of (1), 2 (or 3) stamens, borne by an andropodium or androphore (or this interpreted as the staminal filaments fused for about one-half their length); anthers introrse, 4-locular, longitudinally dehiscent; pollen grains in dyads. Gynoecium 2-carpellate, syncarpous; styles 2, simple, equal, free, the stigmata indistinct; ovary superior, 2-loculate, the abaxial locule larger; ovules many, anatropous on a thick, fleshy, axile placenta. Fruit a [6- or] 8-ribbed, septifragal, 2-valved capsule, the smaller, adaxial valve caducous, the larger, abaxial valve persistent, the enlarged placenta and seeds becoming detached; seeds numerous, minute, with an outer mucilaginous layer (when moistened). TYPE SPECIES: *P. ceratophyllum* Michx. (Name from Greek, *pous*, *podos*, foot, and *stemon*, stamen, in reference to the stamens apparently supported by a pedicel: "stemonia pedicello suffulta.") — RIVERWEED.

A primarily tropical genus of 17 or more species of North and South America, and perhaps India and Ceylon: *Podostemum ceratophyllum* in eastern North America, Hispaniola, and Honduras; *P. ricciiforme* (Liebm.) Royen in Mexico and Costa Rica; and 15 species distributed from central Brazil to Uruguay, Paraguay, and northern Argentina. Species attributed to this genus have been described from Africa, Madagascar, India, and Ceylon, but all except two, *P. subulatum* Gardner (Ceylon and southern India) and *P. Barberi* Willis (southern India), have been excluded (cf. Engler, 1915; Willis 1902b, c; Hall). The taxonomic disposition of these two species appears to be unresolved, but it may be worth noting that their leaves are spirally, rather than distichously, arranged and lack stipules.

Podostemum ceratophyllum, the only species of the family in eastern North America, has an unusually broad distribution, extending northward to New Brunswick, Quebec, and Ontario, and southward to Georgia, Alabama, Mississippi, Louisiana, southeastern Oklahoma, and western Arkansas, and with disjunct localities in the Dominican Republic and (as var. *circumvallatum* Royen) in Honduras. It is of local occurrence and is extremely variable in habit, especially in size and dissection of the leaves. One extreme with lax, elongate leaves has been named f. *abrotanoides* (Nutt.) Fassett, and the opposite extreme with coarse, rigid leaves is f. *chondroides* Fassett, the author of the combinations acknowledging that the two are not geographically distinct and are connected by a series of

between filaments, $\times 6$; f, flower immediately before anthesis, $\times 6$; g, flower at anthesis, $\times 6$; h, cross section of ovary to show unequal locules and axile placentation, $\times 12$; i, part of stem with nearly mature fruit to upper left (spathella mostly broken away), immature fruit with withered, persistent anthers to upper right, leaf base and young leaf to lower right, $\times 6$; j, mature fruit before dehiscence, $\times 12$; k, fruit after dehiscence, larger valve of capsule persistent on pedicel, $\times 12$; l, placenta removed from fruit, $\times 12$; m, seed, moistened to show mucilaginous seed coat, $\times 25$; n, dry seed, $\times 25$.

intermediates. Whether this variation is genetic or ecological is largely unstudied. Hammond found, however, that at Difficult Run, Virginia, three forms grew side by side, forming colonies of various sizes, the plants of a colony being usually uniform in size and structure. When plants of the two extremes were transplanted to two localities in Maryland, they grew well and retained their original characteristics during an observation period of several weeks.

The extraordinary life history of *Podostemum ceratophyllum* was studied by Hammond, who observed the entire cycle in Maryland and Virginia, with the exception of seed germination. Growth of roots and shoots begins in the spring from the bases of plants of the previous season; by June flower buds are formed in the axils of leaves, where they remain inclosed in the spathella as long as the plants are submerged. If the water level subsides, exposing the plants, the pedicel promptly elongates and the spathella ruptures, revealing the flower. Self- or perhaps wind-pollination occurs, and within a few days the seeds are mature and shed from the open capsule, where they adhere to the surrounding dry rocks by means of mucilaginous seed coats. In our area, where wet and dry seasons are indistinct, the plants may remain submerged through an entire summer, never flowering, but growing vegetatively and propagating by regeneration from pieces of roots, stems, or leaves that have broken from the parent plant.

Seed germination apparently has not been observed in *Podostemum ceratophyllum* but is probably like that of *P. subulatum* (cf. Willis, 1902c, p. 329) and many other genera of the family. With the rise in water level the hypocotyl emerges from the seed, bends downward, attaches itself to the substrate by root-hair-like rhizoids and expands to form a larger area of attachment. The seedling becomes erect, cotyledons and primary leaves appear in two ranks, and the primary axis then stops growing. No developed primary root has been reported for any member of the family, and the secondary root is adventitious from the base of the hypocotyl. The root is dorsiventral, and in *P. ceratophyllum* there are only two rows of lateral roots, all of which retain this symmetry. Branches are produced in pairs a short distance behind the root growing point. The roots attach themselves by root hairs and by disclike or fingerlike haptera that arise exogenously from the underside of the root, usually under the base of each shoot. The haptera are entirely parenchymatous, have a terminal growing point, and lack vascular tissue. They are believed by some to be derived phylogenetically from the root, by others to be similar to tendrils in origin. The shoots grow out transversely to the root and more or less erectly from the substrate.

There is no stem growing point, each of the two-ranked leaves arising from the base of the next older leaf in its rank. Each leaf has an intrapetiolar stipule. Lateral branches of the shoot are not axillary within these stipules but arise at the base of the abaxial side of the leaf (i.e., on the side opposite the stipules) and are covered by a stipulelike structure formed on this same side of the leaf. Stomata are completely absent,

and the epidermal cells of the root, as well as of the leaves, contain chlorophyll.

The only chromosome number reported for the genus is $2n = 40?$ in the Ceylonese and southern Indian *Podostemum subulatum*.

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Under family references see especially MAGNUS & WERNER (pp. 285–292), VAN ROYEN (1951; 1954, pp. 228–244), TULASNE (pp. 129–132), WARMING (1881, pp. 1–34), and WILLIS (1902b; 1902c, pp. 327–340); see also GARDNER, MARTIN, NASH, SPRAGUE, SUBRAMANYAM, and WEDDELL.

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S. A. G.

DEPARTMENT OF
BIOLOGICAL SCIENCES
KENT STATE UNIVERSITY
KENT, OHIO 44242

C. E. W.

ARNOLD ARBORETUM
HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS 02138

ADDENDA

The following family references contain material of general biological interest.

GRUBERT, M. Podostemaceen-Studien. Teil I. Zur Ökologie einiger venezolanischer Podostemaceen. *Beitr. Biol. Pflanzen* 50: 321–391. 1974 (15 July 1975). [Many important observations, especially in the Río Caroni, Venezuela, on *Apinagia multibranchiata*, *Mourera fluviatilis*, *Rhyncholacis penicillata*, and *Weddellina squamulosa*. Includes morphology, habitat, conditions favoring flowering, structure, and behavior of inflorescences, fruit development (these species requiring at least three weeks), and seed dispersal (by wind).]

SCHNELL, R. Contribution à l'étude des Podostémacées de Guyane. *Adansonia* II. 9: 249–271. 1969. [List of species collected in Guyana, remarks on taxonomic characters and variability and on ecology and biogeography.]

——— & G. CUSSET. Remarques sur la structure des plantules des Podostémacées. *Ibid.* 3: 358–369. 1963.